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Effects of food type and number of feeding sites in a tree on aggression during feeding in wild Macaca fuscata

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Food type and the number of feeding sites in a tree affect aggression during feeding in wild Japanese macaques

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Abstract It is important to understand the effects of ecological factors on aggression during feeding in order to link habitat characteristics to competitive regime and social relationships. Multiple habitat characteristics are likely to affect aggression, but few studies have examined the effect of multiple factors on within-group competition simultaneously. I examined the effect of eight factors on aggression during feeding in wild Japanese macaques living in a coniferous forest in Yakushima: density of the tree species, feeding time, number of feeding sites within a feeding tree, number of co-feeding animals, within-tree macaque density, food type, rank and sex of the focal animal. When macaques co-fed with other individuals, food type, the number of feeding sites and their interactions significantly influenced aggression. Aggression increased when macaques ate fruits/seeds when compared to other foods and as the number of feeding sites decreased. Primate socioecological models highlight the importance of clumped distribution of food patches as a correlate of within-group contest. However, this study indicated that primatologists need to pay attention to the factors related to the current feeding tree (food type and feeding tree size with respect to monopolizability) in addition to the distribution of food in the entire home range.

Keywords aggression; co-feeding; food distribution; monopolizability; Yakushima

Introduction

Patterns of aggression in defense of food resources during feeding affect competitive regimes (Janson 1985), which in turn affect female social relationships (van Schaik and van Hooff 1983; van Schaik 1989). Animals

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make decision on whether to defend a food patch or not based on the distribution of available food resources (Pruetz and Isbell 2000; van Schaik 1989). Most primate socioecological models predict that a clumped food distribution and the monopolizability of a food patch enhance contest competition (Sterck *et al.* 1997). Furthermore, high-quality patches of intermediate size relative to group size can also lead to within-group contest competition (Koenig 2002; van Schaik and van Noordwijk 1988). However, conceptualizing the 'distribution' of food resources is problematic, and it remains unclear at which level food distribution affects the likelihood of aggression among wild primates (Isbell and Young 2002).

In order to reveal a biologically meaningful scale of food distribution, it may be useful to clarify the area within which foods can be monopolized by one individual. Wittig and Boesch (2003) categorized the foods of female chimpanzees into monopolizable foods, such as meat, nuts cracked by stone hammers, water holes, and ant eggs and non-monopolizable foods and showed that chimpanzees exhibited more aggression when eating monopolizable foods. However, this kind of qualitative categorization is not always applicable to other species. Vogel and Janson (2007) defined the area of one feeding site within a feeding tree as 200 m^3 (a sphere with a radius of 3.63 m), based on the maximum number of animals which can occupy a food patch of a given size, and showed that the total number of available feeding sites was negatively correlated with the frequency of agonistic interactions in capuchin monkeys. Furthermore, experimentation illustrated that food monopolization by captive rhesus macaques depended upon inter-food distances (Chancellor and Isbell 2008; Mathy and Isbell 2001). Captive rhesus and long-tailed macaques were able to

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monopolize foods within a distance of 1 m (Mathy and Isbell 2001; Schaub 1995). Similarly, wild Japanese macaques in Yakushima exhibited aggression only when inter-individual distances were less than 1 m (Furuichi 1983).

The availability of alternative resources (e.g. feeding sites, other feeding trees) may also affect the likelihood of aggression (Saito 1996; Vogel and Janson 2007). For example, when only a few alternative feeding sites/trees are available, animals must increase the time allotted to searching for an alternative food source if displaced, and thus they are more likely to exhibit aggression in defense of such resources. Food size affects the likelihood of aggression in captive macaques positively, either because vulnerability to aggression increases due to long processing time or because large foods are more attractive to other individuals (Chancellor and Isbell 2008; Mathy and Isbell 2001). The number of co-feeding animals also affects the occurrence of aggression positively (Robbins 2008).

In summary, monopolizability, availability of alternative resources (either inside or out of the feeding tree), feeding time, food quality, and the number of co-feeders have been suggested to affect aggression. Among primate studies, only Vogel and Janson (2007) have investigated all of these factors simultaneously, in their case for capuchin monkeys. Robbins (2008) also analyzed multiple factors for mountain gorillas, including number of co-feeders, tree size and feeding time, but did not study the effect of other feeding trees and food quality and did not investigate tree size with respect to monopolizability. Mitchell *et al*. (1991) suggested that the difference in aggression frequency between two *Saimiri* species was due to ecological factors (e.g. tree size); however, they did not analyze this quantitatively. Current

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knowledge of the relative importance of ecological factors that might affect aggression is clearly limited. Primate socioecological models hold that food conditions determine a competitive regime, at least partly by way of aggression during feeding, but this assumption has rarely been tested and more work is needed to reveal the critical characteristics of food resources which influence within-group aggression during feeding (Isbell and Young 2002).

In this study, I examine the occurrence of aggression during feeding in wild Japanese macaques with respect to six factors that describe the characteristics of food patches: density of conspecific food trees, feeding time, food type, number of feeding sites per tree, number of co-feeding animals, and within-tree macaque density. In addition to these external (ecological) variables, I also examined animal rank and age of focal animal in order to elucidate the possible effect of social factors. I test the following predictions regarding the influence of these factors on rate of aggression during feeding. No specific predictions was made concerning the effect of age.

1) Density of alternative conspecific food trees: I predicted that the frequency of aggression would increase with lower density of the food tree species. When eating low-density food items, macaques are predicted to defend the food tree against competitors because there are no alternative conspecific food trees available. I examined the density of only conspecific food trees because each food species has its own particular nutritional properties, and thus macaques may selectively eat each species accordingly. Although the nutritional property varies even within species, between-species variations are larger than within-species variations (Chapman *et al.* 2003). In addition, in the study forest, food tree density is generally very high throughout the year (ca. 4000 trees/ha)

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when all food species are combined (Hanya 2004a). Therefore, it seems unlikely that the total availability of food trees affects the likelihood of aggression.

2) Feeding time: I predicted that the frequency of aggression would increase with longer feeding time.

3) Food type: I predicted that the frequency of aggression would increase when eating fruits/seeds. Macaques in this forest prefer fruits and seeds over leaves and flowers (Hanya 2004b). This preference is likely to relate to the higher nutritional quality of fruits and seeds when compared to other foods (Iwamoto 1982) and the digestive system of Japanese macaques, which is better at digesting non-structural rather than structural carbohydrates (Hanya 2004b). Japanese macaques eat mostly mature leaves rather than young leaves in this forest (Hanya 2004b).

4) Number of feeding sites in a tree: I predicted that the frequency of aggression would increase as the number of feeding sites decreased. When the number of monopolizable feeding sites is small, few other feeding sites are available within a feeding tree, and macaques must defend them against other group members. I also predicted an interaction between the number of feeding sites in a tree and the availability of alternative conspecific food trees, with the effect of the number of feeding sites increasing when the availability of conspecific feeding tree is low.

5) Number of co-feeding animals: I predicted that the frequency of aggression would increase with more co-feeding animals.

6) Within-tree macaque density: I predicted that the frequency of aggression would increase with increased within-tree macaque density. The number of co-feeding animals is influenced by the number of available feeding sites, creating a confounding relationship between the number of feeding sites and

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aggression. For example, in terms of macaque density, a tree with 4 feeding sites and 2 animals is the same as one with 8 feeding sites with 4 animals. In order to reveal which is the most significant factor among number of co-feeding animals, number of feeding sites, or within-tree macaque density, I examined all of these factors.

7) Rank: Higher-ranked individuals are predicted to be involved in aggression in order to confirm and strengthen their dominance (Chancellor and Isbell 2008).

Methods

Study site, subjects, and periods

I conducted the study in a coniferous forest of Yakushima (Hanya *et al.* 2004). The study group of Japanese macaques (*Macaca fuscata*), HR group, contained 24-27 individuals, including 7-9 adult females, 6-7 adult males, 7-10 juveniles and 2 infants. I identified all individuals in the study group using natural markings, such as facial characteristics, loss of fingers, etc. There was a linear dominance hierarchy among group females (Hanya *et al.* 2008). I observed the behavior of 7 adult females in the group from April 2000 to March 2001 (on 107 days) and 5 adult females from October 2003 to January 2004 (on 39 days). Each of the 5 focal animals in the second study period was also observed in the first study period. Two focal females in the first study period were lactating. Other females were not followed because they were less habituated to observer presence.

Term definition

I defined the following four terms:

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176 *Feeding bout*: A feeding bout occurred from the point that a focal animal began
177 manipulating the food item until either leaving the tree or after 20 seconds had
178 passed since last moving in the feeding tree or manipulating the food item.
179 *Aggression*: Aggression included attacks, both overt and subtle threats
180 (open-mouth display and beating branches, ground, etc.) and chases. Subtle
181 acts of avoidance were not included in the definition of 'aggression' for several
182 reasons. First, I was interested in assessing only the active defense of feeding
183 trees. Second, 'avoidance' and 'aggression' are two different behavioral tactics,
184 used by subordinates and dominants, respectively, and it may not be appropriate
185 to lump them together. Third, avoidance may simply represent an animal
186 leaving the patch for other reasons, such as satiation, whereas aggression is an
187 overt and directed behavior that does not easily remain unnoticed. Fourth,
188 avoidance is difficult to detect or record: when eating in large trees, it is difficult
189 to collect data on avoidance that are not biased with respect to tree size.
190 Finally, avoidance may occur at various spatial scales, and it is impossible to
191 record all of them.
192 *Co-feeding animals*: I defined co-feeding animals as those either in or in contact
193 with the tree in which the focal animal was feeding. Though this definition
194 potentially included animals that were not feeding in the tree, in practice it was
195 impossible to determine the behavior of all of the non-focal animals.
196 Regardless, the definition remains meaningful since each individual sharing
197 space with a focal animal in a feeding tree constituted a potential competitor.
198 *Feeding site and monopolizable area*: I defined feeding site with respect to
199 monopolizability. There are two possible ways to define monopolizable area.
200 One is simply to defined the monopolizable area as being within 1 m of a focal

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animal, based on a previous study of this population (Furuichi 1983). Furuichi roughly categorized observed inter-individual distance as 1 m, 3 m, and 5+ m and showed that aggression during feeding occurred only when the inter-individual distance was less than 1 m. Thus he regarded the area within 1 m as monopolizable, and one feeding site constitutes 4.18 m^3 – the volume of a sphere with a radius of 1 m. The second method, employed by Vogel and Janson (2007) yields a similar result. This method plots the maximum number of feeding animals in a tree against a given crown volume, and draws a line such that most points lie below it. The inverse of the resulting slope gives a minimum volume per feeding animal. This procedure gives a minimum monopolizable area for Japanese macaques of radius 1.48 m (Fig. 1).

Behavioral observation

I conducted 1 hour focal samples on 7 adult female macaques between 07:00 and 17:00 for a total of 142 days. When changing between subjects, I selected the animal with the fewest hours of observation up until that point in an attempt to equalize the total observation time for each animal. The observation time for each individual was not biased by time of day. The mean (±SD) total observation time per focal animal was 70±22 hours. The dataset is comprised of 310 hours of 94 days of focal observation in the first study period and 193 hours of 48 days in the second study period.

While focal animals were feeding in a tree, I recorded the onset and end of feeding bouts, the occurrence of aggression involving focal animals (both given and received), the diameter at breast height (DBH) of the tree, the number of co-feeding animals when the focal animal entered the feeding tree (excluding

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dependent infants), and all entries into and exits out of the feeding tree by other animals. I used data from 181 feeding bouts (mean±SD per individual: 25.8±10.1) in which feeding lasted for more than five minutes and there was at least one co-feeding animal. The number of feeding bouts was not biased to particular individuals (the range for the number of feeding bouts per individual was 10-39). No focal animal was in estrous during the observation, so it was unlikely that occurrences of aggression related to mating behavior.

Vegetation and phenology

To assess the density of available food trees, I set a 0.25 ha vegetational plot within the home range of the group to include both ridges and valleys. This plot is smaller than the recommended plot size, which is 5% of the home range: 2.7 km^2*5%=13.5 ha (National Research Council 1981). However, this plot size was too large to be feasible. Tree species diversity in temperate forests is much lower than that in tropical forests (Takyu *et al.* 2005), and species composition, basal area and primary production in this plot do not vary considerably from other plots in the same altitudinal zone in Yakushima (Aiba *et al.* 2007). Seasonal variations in fruit availability in this plot clearly explained the variations in diet and activity budget of this group (Hanya 2004a, b). Therefore, I regarded this plot as being representative of the home range.

I recorded the species and DBH of all trees >5 cm DBH. For 30% of the area of the plot, I recorded the crown height, as well as the largest and smallest width of the crown. To sample smaller trees (i.e. <5 cm DBH), I divided the plot into one hundred 5 x 10 m subplots and randomly selected 10 subplots. In these selected subplots, I recorded the DBH and the species of all

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trees taller than 1 m (all macaque feeding trees were more than 1 m in height). Density of trees (N/ha) was calculated as (Number of trees of DBH>5 cm in the 0.25 ha plot)/0.25+ (Number of tree of DBH<5cm in the 0.025 ha subplot)/0.025, for each species.

I conducted monthly phenological surveys during the entire study period to examine the fruit production of all marked trees (N=705, including the small trees in 0.025 ha subplots). There was a high degree of synchrony in fruit production within species (Hanya 2005). The number of fruiting tree per hectare in any given month was calculated as: (Number of fruiting trees of DBH>5 cm in the 0.25 ha plot)/0.25+ (Number of fruiting trees of DBH<5cm in the 0.025 ha subplot)/0.025, for each species.

Data analysis

I calculated or defined the eight independent variables as follows:

(1) *Density of available conspecific food trees* (tree density, hereafter): For fruit and seed foods, which constitute 50% of the arboreal feeding time (Hanya 2004b), I calculated the density of available trees using the phenological data. Since the number of fruiting trees differed among months, I used the number of fruiting trees in that month for the analysis. For flower foods (17%), phenological data were not available, so I regarded all of the trees in which fruiting was observed in the following months of the year as available flower-food trees. For leafy foods, I regarded all trees of the food species in question available.

(2) *Feeding time*: Duration of the feeding bout (min).

(3) *Food type*: Binary categorization: fruit/seed or other.

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(4) N*umber of available feeding sites within a feeding tree* (#feeding site): I calculated the number of available feeding sites within a feeding tree by dividing the crown volume by 4.18 m^3 and rounding down (Vogel and Janson 2007). For example, if the estimated crown volume was 6 m^3, the number of available feeding sites was 1. I estimated the crown height and crown area of a feeding tree from its basal area ($\pi*(DBH/2)^2$)) using the following regression equation derived from the vegetational data:

Log (crown height; m)=log (basal area, cm^2)*0.269+0.691

Log(crown area, m^2)=log(basal area, cm^2)*0.505-0.064

whereas

Crown area=π* largest width of the crown/2*smallest width/2

I used 127 trees to calculate this equation. It should be noted that this procedure inevitably causes error in the estimation of crown volume when compared to direct measurement. However, the error in the estimation of the number of feeding sites is small because the value is rounded. Finally, I calculated crown volume as:

Crown volume= 1/3*crown area*crown height (m^3) (Janson 1988).

(5) N*umber of co-feeding animals* (#co-feed): The number of co-feeding animals was the average number of animals staying within the same tree throughout the feeding bout of the focal individual. For example, if the number of co-feeding animals was 1 for the first minute, and 2 for the second minute, then the average number of co-feeding animals in the bout was 1.5. I used this value in the analysis, regardless of when aggression occurred during that feeding bout.

(6) Within-tree macaque density (macaque density): #Co-feed divided by #feeding site.

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(7) Rank: Rank of the focal animal: 1 (highest) to 9 (lowest). Rank was determined using submissive behaviors such as grimace and silent supplanting (see Hanya et al 2008 for details). Dominance relationships were linear in this group (Hanya *et al.* 2008).

(8) Age: Since exact age was unknown because habituation started only a few months age of this study, age of the focal animal was categorized as adult or adolescent, from external characteristics following Maruhashi (1982).

Models

I ran a series of generalized linear models (GLM), assuming Poisson distribution, to examine the number of aggression events occurring during feeding bouts. I used the above eight factors as fixed factors. Number of aggression events in each feeding bout (range=0, 1, 2, or 3, mean=0.23, variance=0.30) was not significantly different from Poisson distribution (χ^2=13.0, P=0.11). A positive coefficient means that aggression is more likely to occur with an increase in the independent variable. I selected the best-fit model with the smallest AIC (Akaike's Information Criterion), as follows. First I conducted single-factor analyses, then I conducted all combinations of two-factor analyses, three-factor analyses, etc, only if any of the models including a larger number of independent factors had a lower AIC than all of the models with smaller number of factors. I examined all combinations of two-way interaction terms. The number of explanatory variables (K) was large relative to the sample size (N=181), i.e. $N/K < 40$. Therefore, a correction factor ($2K(K+1)/(N-K-1)$) was added to the AIC scores (Burnham and Anderson 2002). I did not examine macaque density simultaneously with either #feeding sites or #co-feed in the

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same model because the former was calculated from the latter. I excluded feeding trees without co-feeding animals from the model because there was no opportunity for aggression to occur. Collinearity (correlations between independent factors) was not severe in this dataset: the maximum variance inflation factor (VIF) was smaller (2.63) than the cut-off value (5) recommended in Neter *et al*. (2004).

I log transformed all independent variables except food type and age before conducting the GLM. I set the alpha level at 0.05. I used R 2.8.1. (© The R Foundation for Statistical Computing) for statistical analysis.

Results

During feeding bouts which lasted more than 5 minutes with co-feeding animals, the frequency of aggression was 0.92 times/feeding hour (45/48.6), or once every 1 hour and 5 minutes. The average duration of a feeding bout was only 16.1 minutes, and thus I observed aggression in 18% of the feeding bouts (33/181). I summarize statistics of independent factors and crown volume in Table I.

Macaques exhibited aggression more often when they ate fruit/seeds than when eating other foods, and when the number of feeding sites was small. In the best-fit model, the number of aggressions was predicted to increase with small #feeding sites and when macaques ate fruits/seeds (Table II, Fig. 2). In a tree with one feeding site, when aggression was most likely to occur, the expected count of aggression per feeding bout was 0.68 when macaques were eating fruits/seeds and 0.21 when macaques were eating other foods. In a tree with 45 feeding sites, which was the median value, the expected count of

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aggression per feeding bout was 0.051 when macaques were eating fruits/seeds and 0.21 when macaques were eating other foods. The model with the second-smallest AIC only used #feeding sites. The difference in AIC between the best and second best-fit models was 2.4. The addition of other factors to the best-fit model increased AIC by at least 2, and the effect of the added factors was not significant in any model, meaning that the effect of food type and #feeding sites on aggression was fairly robust. In the model that included both tree density and #feeding sites, only #feeding site was significant, and the AIC was larger than the best-fit model by 10.1.

The effect of the number of feeding sites was apparent only when macaques were eating fruits and seeds. Number of feeding sites was significantly smaller for fruits/seeds than other foods (t=3.07, P=0.0025). However, the effect of food type was not merely a by-product of the large number of feeding sites for non-fruit/seed food trees. When I analyzed only fruit/seed feeding, the effect of the number of feeding sites on occurrences of aggression was significantly negative (z=3.90, P<0.0001). When I analyzed only other food feeding, the effect of the number of feeding sites was not significant (z=0.017, P =0.98). Therefore, when macaques ate fruit and seeds in small feeding trees, aggression increased.

Discussion

This study showed that aggression by Japanese macaques in a coniferous forest on Yakushima increased when the number of feeding sites was small and when macaques were feeding on high-quality foods. However, the number of feeding sites did not affect the frequency of aggression when macaques were

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feeding on low-quality foods, such as leaves and flowers. A number of previous studies have identified factors influencing aggression during feeding including monopolizability, availability of alternative resources (either inside or out of the feeding tree), feeding time, food quality, and the number of co-feeders (see Introduction); however, the results of this study indicate the relative importance of these two among the ecological and social factors.

It is easy to imagine how the density of feeding trees might affect the occurrence of aggression: when the density of the feeding tree is high, individual macaques can forage in different trees, and thus avoid conflict. For example, Saito (1996) showed that among wild Japanese macaques in Kinkazan, aggression over food occurred only with respect to low-density food species because alternative food patches were seldom available, forcing group members to forage in the same patch. Such a mechanism would affect the likelihood of aggression indirectly via the number of co-feeding animals. Therefore, when the number of co-feeding animals is examined simultaneously, as in this study, the effect of tree density of trees is not apparent. The number of feeding trees and the number of feeding sites within the tree represent different measures of alternative feeding locations. Macaques in the present study seemed to respond only to the latter, which is perhaps a more cogent factor influencing an individual's behavior.

In terms of food type, aggression was more likely to occur when feeding on fruits and/or seeds, as predicted. Because the number of feeding sites in fruit/seed feeding trees was smaller than that of other food trees, there remained a possibility that the effect of food type was only a by-product of the number of feeding sites. However, the number of feeding sites did not affect aggression

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401 when only low-quality foods were analyzed. It is not clear whether limited
402 distribution or high nutritional quality is the cause of frequent aggression during
403 fruit/seed eating. However, because tree density did not affect aggression, high
404 nutritional quality seems to be more important.
405 The number of feeding sites within a feeding tree affected the
406 occurrence of aggression while foraging on fruits and seeds. When only a few
407 feeding sites existed within a fruit/seed feeding tree, macaques defended the
408 feeding site against other members. These results are in accordance with
409 Vogel and Janson (2007), who showed that agonism in capuchin monkeys
410 increases when fewer feeding sites are available. The authors based these
411 conclusions on the result that number of feeding sites was negatively related to
412 aggression. The average number of feeding sites was much larger for
413 Japanese macaques (56, Table I) than for capuchins (2.15=429 m^3 crown
414 volume/200 m^3 per one feeding site). However, the data in this study included
415 considerable number of small trees having only one or two feeding sites (21 and
416 6 among 181 feeding trees, respectively). These trees in Yakushima were
417 small enough to provoke aggression when there were multiple co-feeding
418 animals.
419 Vogel and Janson (2007) defined monopolizable areas as 200 m^3, a
420 sphere with a radius of 3.63 m, which was much larger than our definition based
421 on a radius of 1 m. Because macaques are larger than capuchins, we would
422 expect the opposite. This is not because of the different definitions of
423 monopolizable areas, because using the same definition of monopolizable area
424 for Japanese macaques gives 1.48 m. Definitions aside, macaques and
425 capuchins may tolerate different levels of proximity to other individuals during

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feeding. Because of the smaller feeding tree size for Japanese macaques (mean+SD: 172+13 m^3) than for capuchins (429±24 m^3; Vogel and Janson, 2007), macaques would need to exhibit greater levels of tolerance in order to keep the frequency of aggression (and thus injury or time costs) at the same level as capuchins. Another possibility is that the food distribution within a feeding patch is different within a feeding patch in Costa Rica (Vogel and Janson's (2007) study site) and Yakushima. Further investigations are required to understand this difference in monopolizable area between the two species. For example, the monopolizable area could be compared directly for the two species using a feeding experiment, giving attractive foods at two places at varying distances. If the average size of feeding tree affects the tolerance levels, it would be useful to compare different populations of the same species having different sizes of feeding trees.

Possible limitations to the analysis presented here include (1) small R^2 value, (2) other possible factors affecting aggression and (3) small sample size. (1) *Small R^2 value*: The value of R^2 was small (0.072), indicating that although the model was highly significant, it only explained a small portion of the occurrence of aggression. Thus, knowing the food type being eaten and the number of available feeding sites was still unlikely to help one predict when aggression will occur. The most likely reason for this is the overall low frequency of aggression, which occurred in only 18% of the feeding bouts. Aggression was a rare behavior, and macaques often did not exhibit aggression under the circumstances when the likelihood of aggression increased (e.g. feeding on fruits and seeds in small trees). The model was highly significant, thus perhaps these factors really do account for much of the actual variation in

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aggression in spite of the low R^2 value. The results of this study still have values because they can point out the importance of food type and number of feeding sites on the occurrence of aggression, which would be useful information for future studies of aggressive behavior.

(2) *Other possible factors affecting aggression*: Other food characteristics that could not be incorporated in the model, such as patch depletion time (Isbell and Young 2002), satiation level (Janson and Vogel 2006), and fruit abundance within the fruiting tree, might also affect the occurrence of aggression. Patch depletion time does not seem to affect this population because macaques often leave patches before feeding speed decreases (Hanya, unpublished data). Although Janson and Vogel (2006) proposed a procedure to estimate satiation level by the time since ingestion and amount of ingestion, it was not applicable to this study because data on previous feeding were not available.

(3) *Small sample size*: Considering the low frequency of aggression, the sample size (*N*=181 feeding bouts) was not large. Therefore, it is possible that the effect of other significant factors was not detected due to the small sample size. However, the effects of food type and number of feeding sites can be considered the largest because the effects were clear even in this small sample size.

In conclusion, the present study indicates that both food type and the number of feeding sites within a feeding tree affect the occurrence of aggression. Japanese macaques are more likely to engage in conflict when they forage on 'high-quality' (in terms of energy content and limited availability) fruit/seeds and when alternative food resources (feeding sites) are not available within the feeding tree. Primate socioecological models have highlighted the importance of clumped distribution of food patches as a correlate of within-group contest

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476 (Isbell and Young 2002; Sterck *et al.* 1997). However, this study indicated that
477 primatologists need to pay attention to the factors related to the current feeding
478 tree (food type and feeding tree size with respect to monopolizability) in addition
479 to the distribution of food in the entire home range.
480

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591 Legends to figures

592 Fig. 1. Relationship between the crown area of the feeding tree and the
593 number of feeding animals in the tree. The thick line is drawn such that
594 most points lie below the line, in order to assess the maximum number of
595 animals that can feed for a given size. The dashed line is the one used
596 by Vogel and Janson for capuchins (Vogel and Janson 2007). Because
597 the line for Japanese macaques is steeper than the one for capuchins,
598 more individuals can feed in a feeding tree of a given size for Japanese
599 macaques than for capuchins.

600 Fig. 2. Number of feeding bouts with respect to number of feeding sites. Note
601 that the x-axis is log-scale. (a) Fruit/seed, aggression absent. (b)
602 fruit/seed, aggression present, (c) other foods, aggression absent and (d)
603 other foods, aggression present.

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Table I. Statistics of fixed effects of the generalized linear mixed model (GLMM)

Factor	Mean	SD	Min	Max
Density of available conspecific food trees (/ha)	184	686	1	3494
Feeding time (min)	16.7	13.3	6.03	60
#Feeding sites	56.3	58.4	2	274
#Co-feeding animals	4.23	3.36	1	16
Within-tree macaque density (#co-feeding animals/#feeding sit	0.08	0.22	0	2
Crown volume (m^3)*	229	243	0.03	1139

605 *: Not included in the GLM

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Table II. Correlation coefficients in the best-fit generalized linear model on the number of aggression during feeding in trees.

Independent factors	Coefficient	SE	*P*
Food type (fruit/seed)	1.55	0.74	0.035
#Feeding sites	0.54	0.14	<0.0001
Interaction food type*#feeding sites	-0.54	0.22	0.014

df =177, P< 0.0001, R^2 =0.072, AIC=209.8

All independent variables except food category were log transformed, then z-standardized.
606 Positive coefficient means aggression is more likely to occur with increasing independent va

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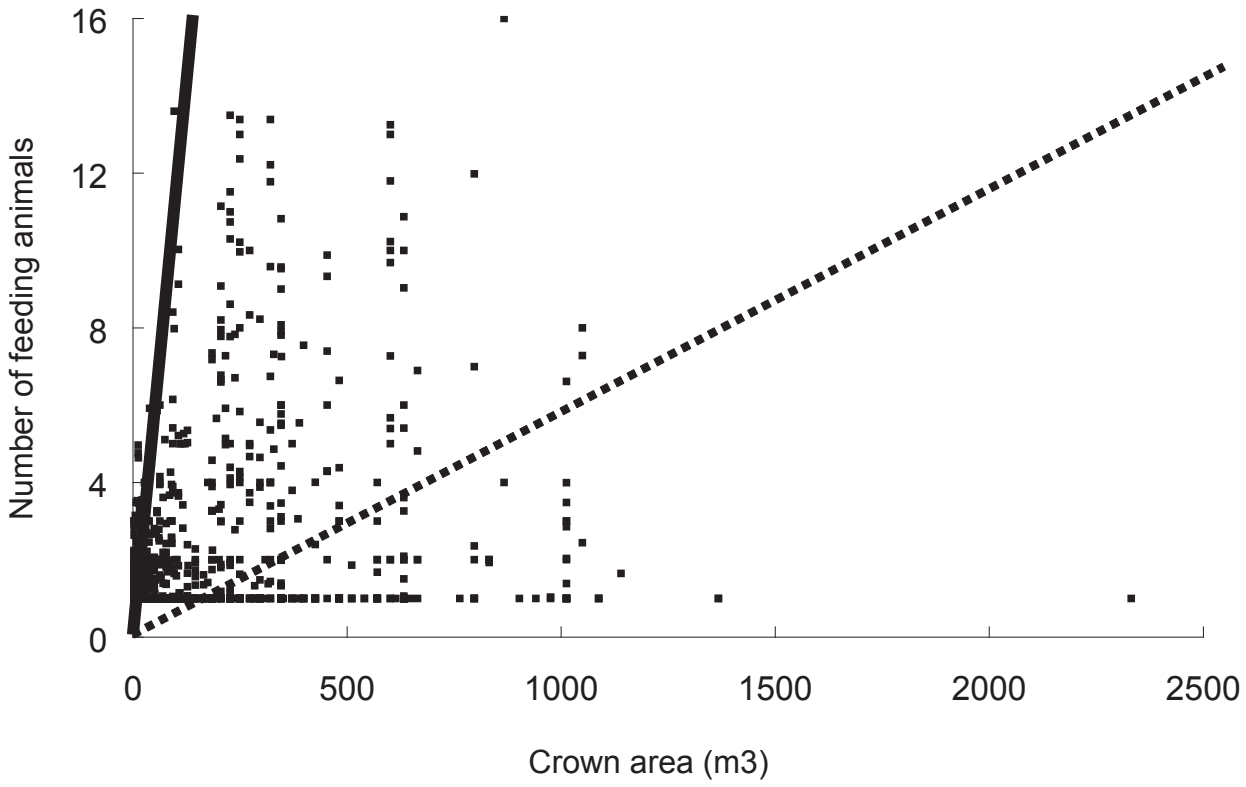

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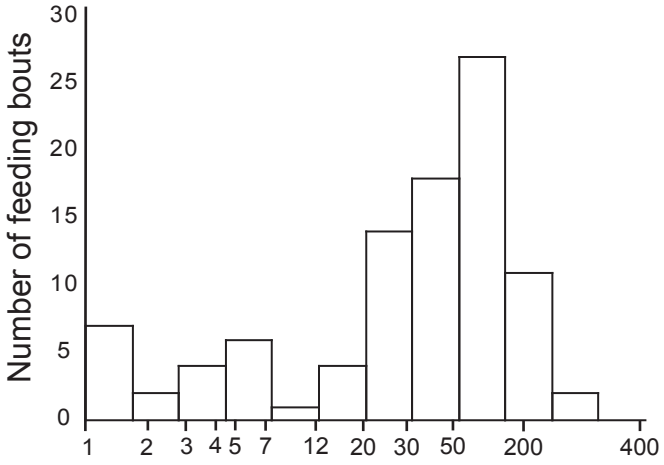
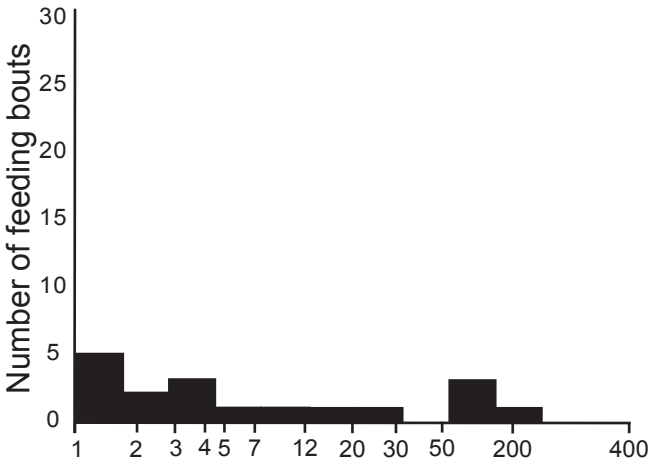
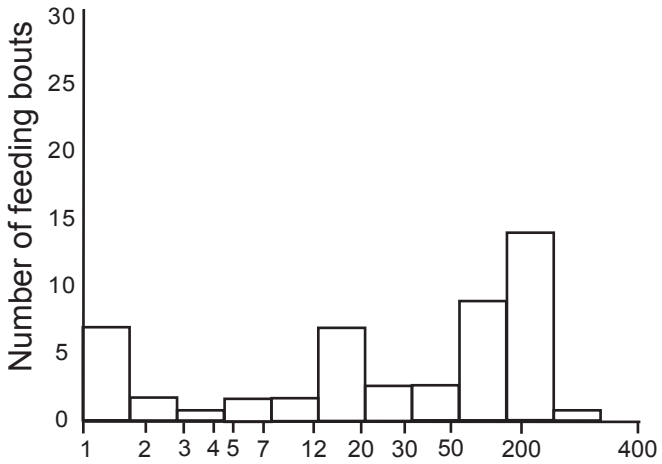
(a) Fruit/seed, aggression absent



(b) Fruit/seed, aggression present



(c) Other food, aggression absent



(d) Other food, aggression present